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The Fecundity of Atlantic Salmon (*Salmo salar* Linn.)

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EDINBURGH: HER MAJESTY'S STATIONERY OFFICE
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The functions of the Scottish Home Department relating to fisheries were transferred on 1st April, 1960 to the Department of Agriculture for Scotland, which will in future be known as the Department of Agriculture and Fisheries for Scotland.

The Fecundity of Atlantic Salmon (*Salmo salar* Linn.)

INTRODUCTION

There is hardly any information on the fecundity of Atlantic salmon and that which is available is not of a detailed nature. A number of workers (Day, 1887; Calderwood, 1930; Menzies, 1931, 1949) have quoted values of from 600 to 900 for the average number of eggs per pound weight of female fish. These values have been based on a few random counts and are only approximate. Other more detailed estimates also showed a wide range. Nall (1930), from an examination of 194 salmon stripped at a hatchery, gives an estimate of 640 eggs per pound weight, while Jones and King (1946) give a range, based on the egg counts of 12 fish from the Cheshire Dee, of from 419 to 770 eggs per pound weight. Elson (1957), in his estimate of potential egg deposition in the Pollett River, uses the figure of 800 eggs per pound live weight of female and Jokiel (1958) found 1400 eggs per kilogram body weight in salmon from the Vistula.

Data available on the fecundity of the Pacific salmon *Oncorhynchus* show that differences have occurred in the egg counts of the same species from different areas (McGregor, 1922, 1923; Aro and Broadhead, 1950). McGregor *(loc. cit.)* was able to detect differences in the number of eggs and pyloric appendages of the chinook salmon *(Oncorhynchus tschawytscha)* in the Sacramento and Klamath rivers of California, but Belding (1940), carrying out a similar study on Atlantic salmon from the Gulf of St. Lawrence area, found that fecundity of fish from different rivers varied little. Rounsefell (1957), in an analysis of available material on the fecundity of North American Salmonidae, suggested that use of the total number of females as a measure of reproductive potential may introduce considerable error. From their work on five Pacific species Foerster and Pritchard (1936, 1941) concluded that the number of eggs laid should not be estimated from the lengths or weights of the fish owing to year to year sampling variations in the relationships between eggs and length and eggs and weight. To get a proper estimate of egg deposition not only in any river system, but on any particular spawning ground, they advocate an actual count on an adequate sample annually. However, the number of counts required to provide an estimate with a smaller sampling error than that obtainable from an average yearly relationship was not considered by these authors and this may not in reality be a good recommendation.

No data are available to show whether conclusions drawn on fecundity of Pacific salmon also apply to Atlantic salmon. The purpose of the work described in this paper was to find whether a reasonably accurate estimate of fecundity could be obtained and if possible to derive a formula, or formulae if differences in fecundity between rivers were found, to be of practical use in estimating the spawning potential of known upstream runs of fish.

MATERIAL

Egg counts made in 1957, 1958 and 1959 on salmon from six Scottish rivers are analysed in this paper. The sample sizes and their distribution over the six rivers during these years are given in Table 1.

Eggs were obtained by stripping and also from the ovaries of dead fish. The majority of the fish stripped during this experiment were caught in traps situated in the upper reaches of each river system and these fish were kept in impoundments until ripe. The maximum period of impoundment was four months. At spawning time the fish were examined approximately twice a week and any ripe fish were removed and stripped.

Two methods of estimating the number of eggs from stripped fish were employed in 1957. The method used for the samples from the rivers Blackwater, Garry and Conon was to strip the fish into separate basins. The eggs were then fertilized, washed and allowed to harden after which water was removed from them by filtering; each sample was filtered for the same period of time. The numbers of eggs were

TABLE 1

Number and Length of Salmon in Samples Classified by Rivers and by Years

River	Year	Number of Fish	Range of Length (cm)	Average Length (cm)
Blackwater	1957	43	47·5-76·0	63·7
	1958	31	51·0-80·0	66·9
	1959	53	50·8-87·0	66·6
Dee	1957	29	57·0-92·0	72·4
	1958*	39	49·0-93·0	70·7
	1958†	35	62·5-88·5	68·7
	1959	57	61·0-87·0	69·2
Lyon	1958	21	53·0-84·0	68·6
	1959	48	67·5-89·0	73·8
Meig	1957 & 1958	10	58·0-78·5	68·6
Conon	1957, 1958 & 1959	13	57·5-73·0	64·7
Garry	1957, 1958 & 1959	23	66·5-95·0	83·8

*Dead fish only †Stripped fish only

estimated by a ratio method described by Burrows (1951). The method used for the samples from the River Dee employed an egg counting device similar to that described by Lindroth (1956). This method of counting the eggs from stripped fish was adopted for all samples collected in 1958 and 1959. The fish from the Blackwater, Garry and Conon were stripped by a different worker at each place, but the fish from the Lyon and the Dee were stripped by the same worker. The same workers did the stripping each year at each site.

Besides counts obtained by stripping, counts were also made on dead salmon from the Blackwater in 1957, 1958 and 1959; from the Conon in 1957 and 1958; and from the Dee in 1958. All the samples from the Meig were from dead fish.

The method of treating the ovaries of the dead fish was that used by Simpson (1951). The left and right ovaries of the dead fish from the Blackwater were weighed before treatment.

The average diameter of random samples of ten fertilized eggs were taken from fish stripped on the Garry and Blackwater in all three years and on the Lyon and Dee in 1958. The average egg diameters were obtained from measurements of the total length of the ten eggs placed together on a grooved measuring board.

Lengths of all fish, from the tip of the snout to the fork of the tail, were measured to the nearest half centimetre.

Weights (in pounds) of salmon taken in the Blackwater, the Meig and the Conon were also recorded in 1957 only.

FECUNDITY

(*a*) Form of Relationship between Egg Number, Length and Weight

The present observations on Atlantic salmon confirm those made on Pacific salmon (Ricker, 1932; Foerster and Pritchard, 1941; Rounsefell, 1957) that there is an increase in egg count with increasing size of fish. Previous workers have used a variety of regression formulae to describe this relationship. A graphical analysis of the data discussed here indicated that over the range of sizes encountered (see Table 1) the observations could be fitted equally well by a linear relationship between either the numbers of eggs and length or between the ordinary logarithms of these quantities. From the statistical viewpoint the latter form is to be preferred for, as is quite common with biological material, the variability increases as the egg count becomes higher. In fact, the observed standard deviation increases approximately

linearly with the mean. In such cases a logarithmic transformation of the observations largely removes the dependence of standard deviation on mean. This is evident in Table 2 which shows the standard

TABLE 2

Effect of Logarithmic Transformation on Standard Deviation of Egg Counts (River Blackwater)

Length	No. of Observations	Mean Count	Stand. Dev. Ordinary	Stand. Dev. Log. values
55	11	2525	460	0·0748
55-	35	3341	598	0·0805
60-	13	4192	668	0·0655
65-	19	4473	796	0·0833
70-	29	5247	1156	0·1204
75	20	6865	1230	0·0705

deviation and mean in 5 cm length groups both for the original observations and their logarithms for data from the river Blackwater.

In the final analysis of the data, where length and egg number only were used, relationships of the form

$$\log_{10}N = a + b \log_{10}L$$

were therefore employed, a and b being estimated in the usual way by least squares. An investigation of the influence on egg number of weight in addition to length was made using, as an obvious extension, a relationship of the form

$$\log_{10}N = a + b_1 \log_{10}L + b_2 \log_{10}W.$$

(*b*) The Use of Weight as a Predictor

In 1957 the weights as well as the lengths of all salmon taken in the Blackwater, the Meig and the Conon were recorded for the purpose of assessing the relative importance of weight in determining fecundity. The use of weight can, of course, be misleading in a fish such as the salmon which loses condition from the time it ceases to feed on approaching freshwater and for this reason it was not surprising to find that, of the two predictors of egg number (viz. length and weight), by far the more important was length. For the Blackwater data, which, being the most extensive, gave the most reliable results, some 75% of the variation in egg number could be accounted for by variation in length alone. The additional information supplied by weight, although statistically highly significant, explained only a further 7% of the variation in egg count. This gain in accuracy does not warrant the additional work entailed in measuring weight as a general practice.

(*c*) Comparison of Methods of Egg Determination

When eggs are obtained by stripping it is to be expected that some eggs will be left in the ovaries. If this bias is appreciable it must be acknowledged and allowed for in any analysis such as the present which includes egg counts obtained both by stripping and from the ovaries of dead fish.

A graphical comparison of the counts obtained by both methods on fish from the Blackwater in 1957, 1958 and 1959 showed no evidence of a difference between methods, any bias in the stripping method on this river being completely obscured by random variation.

The 1958 data from the river Dee, on the other hand, did indicate a difference between the two methods, especially at the lower sizes. The difference between the regression lines fitted to the two sets of counts was found to be statistically significant, the line fitted to counts from dead fish lying above that fitted to counts from stripped fish over almost the entire size range. Although counts on some of the dead fish were made several months before they were due to spawn there is no evidence to suggest that the observed difference might in any way be due to errors introduced by counting eggs which subsequently did not develop. In view of this result the data from dead fish taken from the Dee were analysed separately from the data from stripped fish.

(*d*) Comparisons between Years within Rivers

Sufficient observations were made on salmon from the rivers Blackwater and Dee in each of the years 1957, 1958 and 1959 and from the river Lyon in both 1958 and 1959 to make a study of yearly variations on these rivers profitable. Comparisons for the Dee were made using counts from stripped fish only; that is, counts on the dead fish in 1958 were excluded. In this way the data for the Dee for different years should be comparable.

The method of analysis is illustrated in Table 3 for the Blackwater data. In the upper part of the

Table 3

Analysis of River Blackwater Data

	1957		1958		1959	
	d.f.	S. of S.	d.f.	S. of S.	d.f.	S. of S.
Regression	1	0·5166	1	0·7313	1	0·8027
Error	41	0·1822	29	0·1579	51	0·5462

	d.f.	S. of S.	m.s.
Aggregate Error	125	0·9243	
Pooled Error	121	0·8863	0·00732
Difference	4	0·0380	0·00950

table are shown the regression analyses for each year separately. The pooled error mean square from each analysis and the error mean square obtained in a regression analysis in which all observations are aggregated are shown below, along with the mean square corresponding to the balance of 4 degrees of freedom associated with the two sets of constants in each regression equation, viz. the 3 slopes and the 3 intercepts. On the hypothesis that there are no real year-to-year variations the ratio of this latter mean square to the pooled error mean square is distributed according to the F distribution. The observed value of 1·30 does not exceed the upper 5% point of this distribution, leading to the conclusions that year-to-year variations in the regression lines are not significant.

This was true also of the yearly variations in the equations for the Dee and the Lyon. The regression equations for the Blackwater and the Lyon obtained from the pooled data are respectively

$$\log_{10}N = 2{\cdot}2138 \log_{10}L - 0{\cdot}388 \qquad (1)$$

and

$$\log_{10}N = 2{\cdot}5851 \log_{10}L - 1{\cdot}088 \qquad (2)$$

For the river Dee it is more useful to work not with the regression equation from the pooled data for this river but with the equation obtained from the counts on dead fish in 1958, this equation being free from bias. This equation is

$$\log_{10}N = 2{\cdot}2018 \log_{10}L - 0{\cdot}331 \qquad (3)$$

(*e*) Comparisons between Rivers

The regression equations fitted to each river's data using observations aggregated over all years, except for the Dee, are listed below.

Blackwater	$\log_{10}N = 2{\cdot}2138 \log_{10}L - 0{\cdot}388$
Lyon	$\log_{10}N = 2{\cdot}5851 \log_{10}L - 1{\cdot}088$
Dee	$\log_{10}N = 2{\cdot}2018 \log_{10}L - 0{\cdot}331$
Meig	$\log_{10}N = 2{\cdot}5529 \log_{10}L - 0{\cdot}933$
Conon	$\log_{10}N = 1{\cdot}8103 \log_{10}L + 0{\cdot}379$
Garry	$\log_{10}N = 3{\cdot}2035 \log_{10}L - 2{\cdot}255$

The regression lines are shown in Fig. 1 and indicate the extent of the variation in fecundity between rivers. Highest counts are found on the river Meig while the lowest counts are generally found on the Lyon and the Blackwater. A comparison of the slopes of these lines showed that the differences are not statistically significant. A pooled estimate of the common slope is $2{\cdot}3345 \pm 0{\cdot}1003$ (d.f. = 269).

The distances between the lines fitted with this common slope were tested in an analysis of covariance. This showed that the probability of the distances between the lines being due solely to random causes was very small ($P < 0{\cdot}01$). Consequently there are significant differences in fecundity among the various rivers. The average egg counts corresponding to a fish of length 70 cm, this being the average length of all salmon handled, on each of the six rivers are

Lyon	Blackwater	Garry	Dee	Conon	Meig
4943	5117	5370	5495	5572	6067

These averages were obtained from the values of $\log_{10}N$ given by the following equations with adjustment to correct for bias introduced by the use of the logarithmic transformation.*

Blackwater	$\log_{10}N = 2{\cdot}3345 \log_{10}L - 0{\cdot}607$
Lyon	$\log_{10}N = 2{\cdot}3345 \log_{10}L - 0{\cdot}622$
Dee	$\log_{10}N = 2{\cdot}3345 \log_{10}L - 0{\cdot}576$
Meig	$\log_{10}N = 2{\cdot}3345 \log_{10}L - 0{\cdot}533$
Conon	$\log_{10}N = 2{\cdot}3345 \log_{10}L - 0{\cdot}570$
Garry	$\log_{10}N = 2{\cdot}3345 \log_{10}L - 0{\cdot}586$

Differences between these particular averages were tested, on the logarithmic scale, by means of a multiple range test proposed by Duncan (1955) and modified by Kramer (1956, 1957). This test showed that the Meig differed significantly from both the Lyon and the Blackwater and that these were the only significant differences in the set.

ESTIMATION OF FECUNDITY

In terms of egg number and length the equations relating these quantities assume the form $N = cL^b$ where the power of L is the same for all rivers, $b = 2{\cdot}3345$. This suggests that, for Atlantic salmon, fecundity is always proportional to the same power of the length irrespective of the habitat. The constant of proportionality, c in the above formula, however, differs from river to river. The full curves for the rivers Lyon and Meig, which are the rivers showing the lowest and highest fecundities respectively, are drawn in Fig. 2. This shows clearly the range of the fecundities on the different rivers included in this study. Fecundity on the Meig is 23% higher at any length than fecundity on the Lyon. The difference between these fecundity curves varies from approximately 500 eggs at a length of 50 cm to approximately 2,600 eggs at 100 cm. However the use of a single curve intermediate between these extreme curves for all rivers in this study may be of sufficient accuracy in the assessment of spawning potential in some practical situations.

The sampling errors to which estimates of fecundity, obtained from the relationships derived here, are subject, vary both with the equation used and the length at which fecundity is estimated. Sufficiently accurate approximations to the 95% fiducial limits for the true number of eggs is provided by adding and subtracting 10% to the estimated number.

As egg number does not increase linearly with length the classification of different rivers by reference to the number of eggs per unit fish length is not possible. However, as the power of L in the relationships is constant from river to river, fish of the same length from different rivers may be correctly compared.

The number of eggs per unit weight is frequently employed as a measure of fecundity. Although, as already pointed out, this requires care in application owing to the large variation in weight with condition, it is of interest to see whether fecundity is linearly related to weight. For this purpose the data

*The necessary adjustment to the values of log N before taking the antilogarithm is equivalent, over the range of egg counts in the data, to an average upward adjustment of 2% to the anti-logarithm of the figure given by the equations.

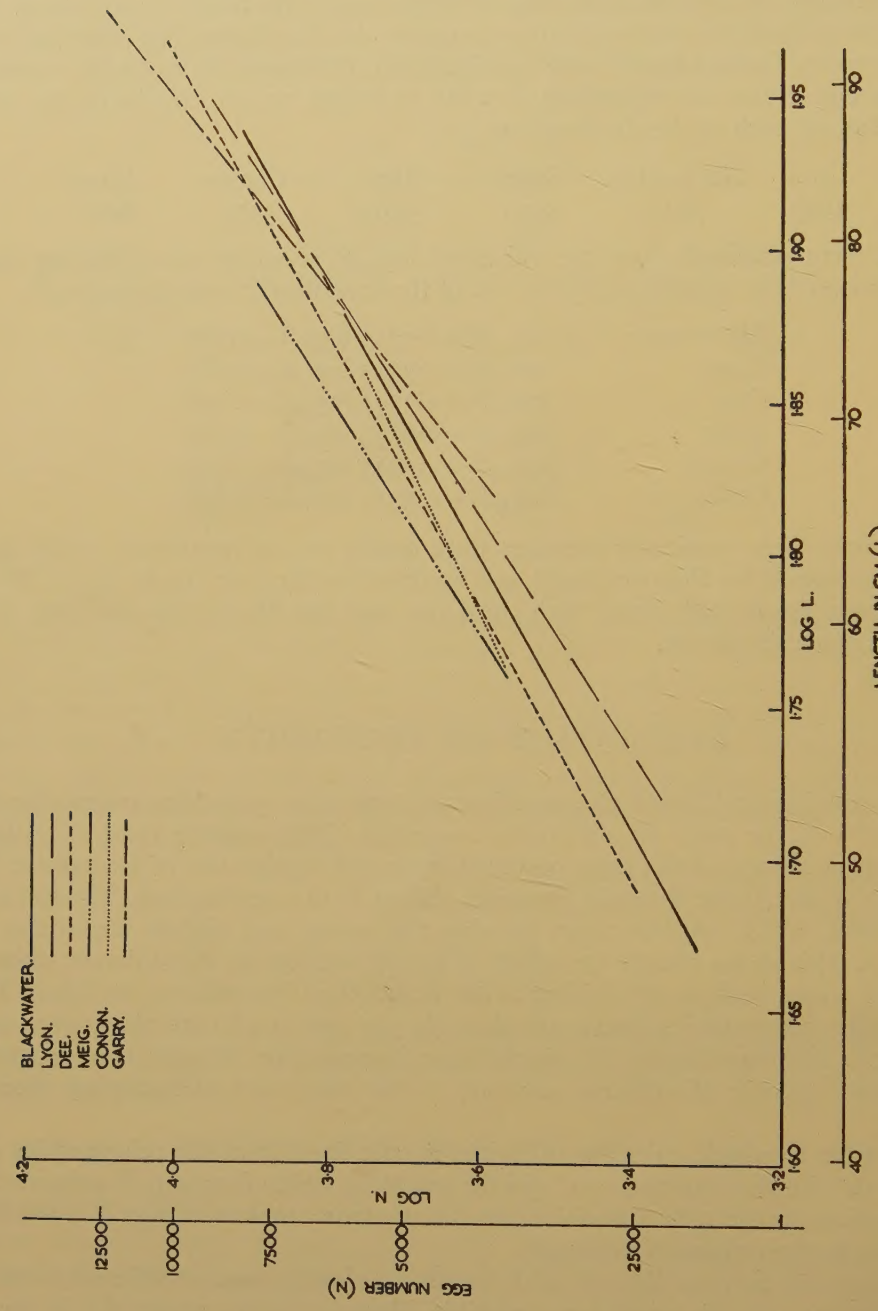

Fig. 1. Individual regressions of log egg number on log fish length

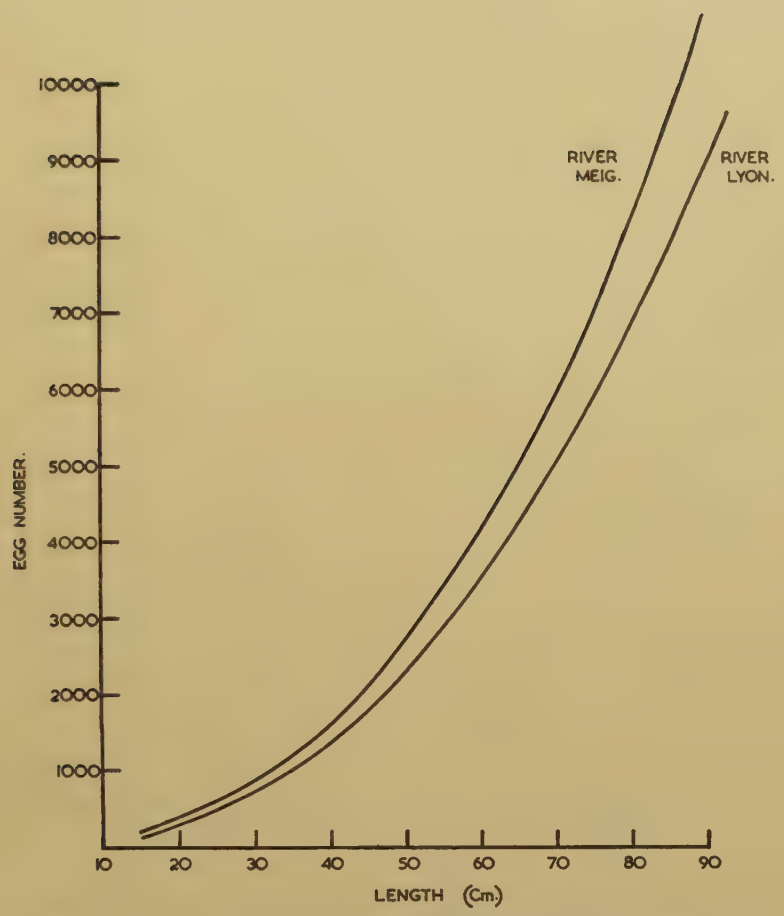

Fig. 2. Fecundity relationships for the rivers Meig and Lyon

from the river Blackwater were used, the weight measurements obtained from that river being from fish all in much the same condition. The power of W was estimated not directly but by inserting the regression of length on weight into the fecundity-length formulae. This gave a value for the power of $0{\cdot}7309 \pm 0{\cdot}0427$ which differs significantly from unity, indicating a non-linear relationship between egg number and weight.

The data on length and weight were also used to provide a length-weight relationship for salmon. This was found to be

$$W = 0{\cdot}00002023\ L^{3{\cdot}000}$$

the standard error of the power of L being $\pm 0{\cdot}1192$ (d.f. $= 41$). In this formula, which should be used for estimating weight from length, W is in lb. and L in cm.

EGG SIZE

The coefficients of correlation between average egg diameter and fish length were calculated for each year separately and in most cases a significantly positive correlation was found to exist between these quantities. The correlation coefficients between egg diameter and log egg number, although positive in most cases, generally did not reach significance. This is due to the fact that although egg number and length are positively correlated egg number is much more variable in the samples than either egg diameter or fish length thereby weakening the association.

When comparing the average diameters of the different groups, therefore, it was sufficient to allow for variations in fish length from group to group but not in egg number. This was done by means of analyses of covariance with length as the independent variate.

Separate analyses of the Blackwater and Garry data indicated significant differences between years. On both rivers the average egg diameters in 1957 and 1958 were similar and significantly lower than the averages for 1959. The difference between the average diameter for 1959 and the average for the pooled 1957, 1958 data were $0{\cdot}49 \pm 0{\cdot}029$ mm for the Blackwater and $0{\cdot}66 \pm 0{\cdot}066$ mm for the Garry. Both differences are significant at the 0·1% level of probability. The slope of the relationships between egg diameter and fish length differed slightly but not significantly for the two rivers, the increase in egg diameter for an increase in length of 1 cm being $0{\cdot}017 \pm 0{\cdot}0054$ mm for the Garry and $0{\cdot}029 \pm 0{\cdot}0039$ mm for the Blackwater.

Owing to the differences between years on the rivers Blackwater and Garry comparisons of these rivers with the Dee and the Lyon were made using the 1958 data only. An analysis of covariance showed significant differences between egg diameters for the four rivers ($P < 0{\cdot}001$). The average egg diameters, adjusted to the average fish length for these rivers, were Dee 5·95 mm; Garry 5·66 mm; Blackwater 5·49 mm; Lyon 5·14 mm. This ranking corresponds with that for the same rivers in terms of average egg count given on page 7 showing again a positive association between egg size and egg number.

The increase in egg size with both size of fish and number of eggs agrees with the findings of Belding *et al.* (1932) and Dahl and Sømme (1944). The rate of increase of egg diameter per 1 cm increase in fish length given by the weighted average of the separate rates for each year and each river is $0{\cdot}024 \pm 0{\cdot}0028$ mm.

The weights of the left and right ovaries of 27 salmon taken in 1957, 14 in 1958 and 16 in 1959, all from the river Blackwater, showed that in each sample the left ovary was heavier than the right in about two-thirds of the fish. The actual results of the weighings are given in Table 4.

TABLE 4

Ovary Weights, River Blackwater

No. of fish with:	1957	1958	1959
left ovary heavier	18	9	10
right ovary heavier	7	4	5
both ovaries same	2	1	1

Rounsefell (1957), in his study of the North American Salmonidae, shows from the available data that the number of eggs in the left ovary is greater than that in the right ovary for total numbers of eggs exceeding about 2,000, and quotes an observation by Kendall (1921) that the left ovary is in general the longer.

DISCUSSION

It has been shown that there is a relationship between the length of the salmon and the number of eggs produced. Although the year-to-year variations in this relationship are not significant, there are significant variations in the relationship between fish from different rivers. The first two of these results call for little discussion, but some comments are needed on the last result.

The method of obtaining the eggs for counting varied from river to river. All the records for the Garry and the Lyon were from fish which had been stripped artificially, those for the Blackwater and the Dee were partly from fish which had been stripped and partly from fish which had died before spawning and those for the Conon and Meig were nearly all obtained from dead fish. When a fish is stripped artificially, some eggs may be left in the abdominal cavity and ovaries and the proportion left may vary for a number of reasons, e.g. the methods used by different workers in different places and small differences in maturity. Comparisons of the counts from dead fish and stripped fish from the Blackwater indicated that the differences were not significant, but similar comparisons for Dee fish indicated that significant differences did occur. All the records from the Blackwater were therefore used in the statistical analyses made in this paper, but only the counts from dead fish from the Dee. As the relationship between counts from stripped and dead fish for the Garry and the Lyon is not known, it is not altogether certain that these records are comparable with those from the other four rivers.

It also should be pointed out that, of the six rivers studied, three (the Blackwater, Conon and Meig) are tributaries of one river system whereas the other three are separate river systems. It seems reasonable to suppose that there are more chances of mixing of stock between tributaries of one river system than there are between the stocks of different river systems so that the existence of significant differences between tributaries suggests that the differences (again significant) between river systems may have less meaning, biologically, than might be supposed.

These comments do not invalidate the statistical findings, but they do suggest that, pending further investigations, more emphasis should be placed on the first two results mentioned at the beginning of this discussion than on the third. To assess the order of magnitude of the potential egg deposition on any river, if great accuracy in the final figure is not essential, it may be sufficient to employ the average equation for all six rivers, namely:

$$\log_{10}N = 2{\cdot}3345 \log_{10}L - 0{\cdot}582$$

where N = number of eggs and L = length (in cm).

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SUMMARY

1. Egg counts made on salmon from six Scottish rivers taken during 1957, 1958 and 1959 are analysed.

2. The method of obtaining the counts is described and the counts are shown to increase with length according to a law of the form $N = cL^b$.

3. Comparisons of counts in different years and from different rivers show that, while the relationship between egg number and length is not subject to significant year-to-year variations, significant differences exist between rivers.

4. The use of the fecundity-length relationships derived is discussed and the sampling errors involved in their use given.

5. The relationship between egg size and length is investigated and it is shown that egg size increases with length and hence with fecundity.

6. A weight-length relationship is derived.

7. The general implications of the results obtained are briefly discussed.

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